Fire and Habitat Interactions in Regeneration, Persistence and Maturation of Obligate-seeding and Resprouting Plant Species in Coastal Heath

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After a fire in January 1991, populations of two obligate-seeding and two resprouting species were followed from seeds sown in dry heath and wet heath on Pleistocene beach sands in the Myall Lakes area. In each type of heath, there were four plots, each with ninety 25 X 25 cm quadrats in which seeds of the four species had been sown in various combinations and surface soil conditions. All four wet-heath plots burned again in January 1998, as did two of the dry-heath plots. The two obligate-seeding species were confined to their respective habitats early in the life cycle; *Acacia ulicifolia* to dry heath by lack of seeds and suitable conditions for seedling emergence in wet heath; *Dillwynia floribunda* to wet heath by failure of its seedlings to survive in dry heath. The two resprouting species were confined to their respective habitats in different ways; *Banksia oblongifolia* by failure of its seedlings to survive in dry heath; *Banksia aemula* by lack of suitable soil surface in wet heath for establishment of its seedlings. In both species of *Banksia*, seedlings require a lignotuber to survive their first fire, and may persist several years without appreciable growth.

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INTRODUCTION

Dispersal, survival and reproduction of individuals underlie patterns of distribution and abundance of species. Fire influences these processes in plant life histories, and moulds patterns evident in fire-prone vegetation across gradients in habitat. In fire-prone vegetation, species of seed plants tend to fall into two groups (Gill 1981), obligate-seeders, those whose adult plants die in fires that destroy their leaf canopies and regenerate after fire solely from seed, and resprouters, some of whose plants survive complete loss of their canopy in intense fires and resprout new canopies after fire from vegetative tissue that is protected from fire. Frequent fires may act selectively and reinforce the respective characteristics of these two groups of plants. In obligate-seeders, high production of seeds, in amount and early availability after fire, would be expected, with the seeds protected from burning, either by being contained in fire-resistant fruits or by dispersal to safe sites in soil and having dormancy that is only readily broken by stimuli connected with the passage of fire. In resprouters, seedlings would be expected to produce at an early stage vegetative parts that survive fire. Pate et al. (1990) showed that seedlings of obligate-seeding species devote much growth to their shoots and early seed production, while seedlings of comparable resprouting species devote a high proportion of their growth to underground tissues including fire-resistant vegetative storage organs. In seedlings of resprouters, production of fire-resistant vegetative tissue typically precedes seed production. In their life histories, seed production is usually considerably delayed compared with related obligate-seeding species.

Obligate seeders probably have simpler relationships linking seed dispersal, germination and seedling establishment in particular environments, their regeneration niches (sensu Grubb 1977), to seed production than do resprouters. Resprouters, while passing through seed dispersal, germination and seedling establishment in particular environments, their regeneration niches, also have periods of persistence as vegetative plants, that though fire-hardy, may or may not become reproductive and produce seed. It is possible that resprouters may simply persist many years as small plants with little net growth. The persistence niche (sensu Bond and Midgley 2001) of resprouters may be wider than conditions under which the plants progress to seed production.

The opportunity arose to observe through time seedlings of obligate-seeding and resprouting species after fire occurred across habitats in fire-prone coastal heath. Such heath occurs in south-eastern Australia on leached siliceous beach sands and dunes deposited during the Pleistocene from South Australia (Specht 1981) to sand islands such as North Stradbroke Island (Clifford and Specht 1979) off the south-eastern coast of Queensland. On the coast of New South Wales, they occur particularly north of Newcastle to the Queensland border (Griffith et al. 2003, Keith 2004). In the Myall Lakes area, heath occurs on a Pleistocene system of beach sands in the Eurunderee Embayment of Thom et al. (1992). On these sands, there is a catenary sequence of soils and vegetation with dry heath on ridges, wet heath on slopes and swamps in periodically waterlogged swales (Carolin 1970, Myerscough and Carolin 1986, Myerscough et al. 1995). Dry heath belongs to the *Banksia serratifolia (aemula)* Alliance of Beadle (1981) and Wallum Sand Heaths of Keith (2004), and wet heath to Beadle's (1981) *Banksia aspleniifolia (oblongifolia)* Alliance and Keith's (2004) Coastal Heath Swamps. Fire has occurred fairly frequently, but over two decades produced no detectable effect in changing the pattern of differentiation of vegetation across the sequence of habitats, though changes with time since fire were clearly evident in the vegetation within habitats (Myerscough and Clarke 2007). Carolin (1970) demonstrated that various species occupy characteristic ranges of habitat in the catenary sequence from the ridges to the swales. Myerscough et al. (1996) and Clarke et al. (1996) investigated in four species how occupancy of their ranges of habitat might arise through dispersal of seed and, after fire, germination and establishment of their seedlings. Seedlings of two species characteristic of wet heath, obligate-seeding *Dillwynia floribunda* and resprouting *Banksia oblongifolia*, did not survive in dry heath, despite their seeds occurring and germinating there (Myerscough et al. 1996). Seed of two species characteristic of dry heath, obligate-seeding *Acacia ulicifolia* and resprouting *Banksia aemula*, were at best rare in wet heath (Myerscough et al. 1996), and, unless the soil surface is artificially disturbed and seeds are buried, germination and seedling establishment did not occur (Clarke et al. 1996). In short, it was largely in regeneration niche (Grubb 1977) that these species appeared to be segregated to their respective habitats, *D. floribunda* and *B. oblongifolia* to wet heath, and *A. ulicifolia* and *B. aemula* to dry heath (Myerscough et al. 1996, Clarke et al. 1996).

Seedlings of the four species were observed beyond the phase of establishment. Establishment of seedlings of *Acacia ulicifolia* and *Banksia aemula* had occurred in wet heath, following experimental manipulation of the soil surface (Clarke et al. 1996). Early survival of seedlings of both obligate-seeding species was related to type of habitat, but in both resprouting species it was related to variation among plots within types of habitat (Clarke et al. 1996). In this paper, ongoing survival of seedlings of the two obligate-seeding species is examined in relation to type of habitat, while in the two resprouting species it is examined in relation to variation among plots within types of habitat.

Fire recurred in six of the eight experimental plots seven years after the fire that immediately preceded the start of the experiment. Survival of seedlings of the two resprouting species through fire could thus be assessed. Benwell (1998) observed lignotubers in seedlings of *Banksia aemula* and *B. oblongifolia* in similar coastal heath and found their growth to be slow seven years after fire. Four years after our experiment started, lignotubers were observed on some seedlings of each of the two species. By using fire-proof tags and measuring sizes and positions of lignotubers, survival of seedlings through their first fire could be assessed in relation to size and position of their lignotubers, if indeed they had been formed. Auld (1987) had found in *Angophora hispida* that seedlings with buried lignotubers survived fire better than those lacking lignotubers or with them exposed above the soil surface.

Ongoing observation of lignotubers and sizes of banksia seedlings was used to try to identify whether they were growing or merely surviving without net growth. One seedling of *Banksia aemula* was observed to flower and set fruit. It was thus possible to see whether a fire-proof stem was required for flowering and seed production as Bradstock and Myerscough (1988) found in juveniles of *Banksia serrata*.

The questions investigated in this paper are:

• Do patterns of early seedling survival in the two obligate-seeding species seen in relation to type of habitat continue into later stages, and how are these patterns related to flowering and seeding?

• How are patterns of seedling survival in the two resprouting species related to characteristics of individual plots?

• What roles do formation, size and position of lignotubers play in the survival through fire of

Table 1. Experimental plot locations and their transect, ridge position relative to coastline, habitat, and fire history since January 1991.

Plots	GDA	Transect	Ridge	Habitat	Fire history	
	32° S 152° E				Jan 1998	Nov 2006
T2W1	29.734' S * 21.125' E	T2	Near	WH	Totally burnt	Totally burnt
T2W3	29.530' S * 21.013' E	T2	Far	WH	Totally burnt	Totally burnt
T3W1	29.162' S * 22.310' E	T3	Near	WH	Totally burnt but some scorched leaves present	Totally burnt
T3W2	29.083' S* 22.250' E	T3	Mid	WH	Totally burnt but some scorched leaves present	Burnt but with some patches unburnt
T2D2	29.594' S* 21.040' E	T2	Mid	DH	Totally burnt	Totally burnt
T2D3	29.500' S 21.026' E	T2	Far	DH	Totally burnt	Totally burnt
T3D1	29.111' S* 22.302' E	T3	Near	DH	Unburnt	Unburnt
T3D2	29.019' S 22.289' E	T3	Mid	DH	Most or less unburnt - one edge slightly scorched	Mostly unburnt – some lightly scorched patches

*, 30 X 5-m plot extends to left of marker post when facing inland; other plots extend to right of post. Dry heath (DH) and wet heath (WH).

seedlings of the two resprouting species?
• Do seedlings of the two resprouting species show appreciable net growth, and under what conditions may they do so?
• Do patterns of seedling growth and survival give evidence of the longterm stability of the patterns observed in the vegetation across habitats of this coastal heath?

METHODS AND MATERIALS

Study area

The heath studied was on sands of a Pleistocene beach system in the Euruderee Embayment of Thom et al. (1992). Twenty-four plots, 3 wet-heath and 3 dry-heath plots in each of 4 transects, were used by Myerscough et al. (1995) to analyse floristic variation in heaths across the system. Each plot was 30 X 5 m with its longer sides parallel to the nearest beach ridge. Eight of the plots, two wet-heath and two dry-heath plots on each of the two central transects, were used in the experiments of Myerscough et al. (1996) and Clarke et al. (1996). Each of these plots (Table 1) was divided into a grid of 150 square-metre cells. Ninety cells were randomly chosen and to each of these cells a 25 X 25 cm quadrat was randomly allocated to a particular experimental treatment. Experimental treatments, including placement of seeds of the four species of this study, are described in Myerscough et al. (1996). These ninety quadrats in each of the 8 plots were the areas in which seedlings that arose in 1991 were observed.

Data collection

Periodic counts of seedlings of *Acacia ulicifolia* and *Dillwynia floribunda* were maintained from 1991 until the fire of January 1998 burned six of the eight plots (Table 1). Between 1995 and 1997, due to the density of stems, especially in wet heath, it became increasingly difficult to count seedlings of *D. floribunda* and *A. ulicifolia* on the small quadrats. Since there was no seedling recruitment apparent during this period, where a greater number of seedlings on a plot was recorded six months after the previous count, the greater number was taken to be correct. After January 1998 until October 2008, individuals of *Acacia ulicifolia* continued to be counted on the unburnt plots T3D1 and T3D2.

In *Banksia aemula* and *B. oblongifolia*, all survivors of the 1991 cohort of seedlings were counted on the eight plots. In November 1995, surviving banksia seedlings were marked with fireproof metallic tags on stainless steel pins placed beside the seedlings. All seedlings of *Banksia aemula* were tagged. In *B. oblongifolia*, many more seedlings were then surviving, and in those quadrats where there was more than one seedling only one seedling in the 25 X 25 cm quadrat was randomly selected and tagged. The proportion of individuals tagged in November 1995 and the number of tagged individuals subsequently surviving were used to estimate the population of surviving seedlings of *B. oblongifolia* in each plot. When no tagged individuals had survived in a plot, it was assumed that the whole cohort of seedlings that had arisen in 1991 in the experimental quadrats of the plot had died.

Lignotuber development was followed on each of the tagged seedlings, noting whether a lignotuber was absent or present. If present, its mean width was recorded from two measurements taken in two directions at right angles, and if it was not entirely buried, the height of its top above the soil surface was measured. After the fire of 1 January 1998, in March 1998 survival of the tagged seedlings was assessed. A seedling was scored as dead if it failed to resprout and live if it had resprouted. Most seedlings that resprouted had done so by March 1998, but a few resprouted later and were identified as alive when scored some months later. In all tagged seedlings, alive or dead, lignotuber presence or absence was noted, and, if present, its mean width was measured and whether its top was buried or exposed. The top was scored as exposed if its height above the soil surface was greater than 1 mm. Survival of seedlings through the fire was assessed in relation to habitat and lignotuber presence and exposure above the soil using 2 X 2 contingency tables and Chi square statistic.

Growth of banksia seedlings between 1995 and 2007 was assessed from lignotuber width and plant height. In *Banksia aemula*, seedlings were deemed to have grown if in October 2007 they were found to have a lignotuber width of over 40 mm or a plant height of greater than 40 cm, while in *Banksia oblongifolia* seedlings with a lignotuber width of over 20 mm were deemed to have grown. Widths of lignotubers of *Banksia aemula* were not easily assessed in a consistent way through time for two reasons. Firstly, although two measurements of width taken at right angles to each other were made on each occasion, not all lignotubers are radially symmetrical. Secondly, the lignotubers form with a thick bark, as in the sister species *Banksia serrata* (Beadle 1940, Bradstock and Myerscough 1988), and this bark may erode so that measured widths of lignotubers may lessen in time. Thus it is possible that some of the seedlings of *Banksia aemula* deemed not to have grown between 1995, or from when their lignotuber formed if it was later than 1995, may actually have grown slightly.

Watertables were observed in the plots between 1991 and 1997, and their depths recorded as described in Myerscough et al. (1996). The fire of January 1998 prevented further observations, destroying tops of the plastic pipes used to observe depths to the watertable on 6 of the 8 plots. The depths given in Table 2 were measured on 23 September 1997, when the watertable was relatively high.

To illustrate key floristic variation observed in 1990 across the plots, the nineteen most abundant species were selected from Appendix II of Myerscough et al. (1995) and listed in Table 2 in the order in which they were sorted in the TWINSPAN analysis given in Appendix I of Myerscough et al. (1995). The nineteen species included *Banksia aemula*, *B. oblongifolia* and *Dillwynia floribunda*. The other species, *Acacia ulicifolia*, whose seedlings were observed on the experimental plots was also included.

The height of the canopy of each of the plots was recorded in September 2005 in ten randomly selected 1 X 1 m cells, except in T2W3 where inadvertently there were only nine cells. In each cell, the species of the tallest plant was noted. At the same time, the degree to which each surviving banksia seedling was shaded by surrounding vegetation was subjectively scored using a five-point scale of shade: 5, >95%; 4, 95-75%; 3, <75-25%; 2, <25% shaded; 1, seedling's canopy unshaded.

Nomenclature

Nomenclature of plant names used follows Harden (1990, 1992, 1993 and 2002).

RESULTS

The plots differed floristically and in depths to the watertable (Table 2). Depths to watertable were greater in dry heath than in wet heath plots ($F_{1,6}$=5.90 (p just >0.05)) and differed markedly among plots within habitats ($F_{6,24}$=299.3 (p<0.001)). The habitats differed in plant species that provide significant cover. Both habitats had shrubs with appreciable

Table 2. Experimental plots and mean (SE) depth (cm) to watertable and mean cover (%) of twenty species (RS, resprouter; OS, obligate-seeder).

Plot	T2W1	T2W3	T3W1	T3W2	T2D2	T2D3	T3D1	T3D2
Watertable	2.0 (0.7)	10.6 (1.1)	2.8 (1.4)	18.9 (1.2)	43.3 (0.6)	26.3 (0.6)	108.8 (2.4)	38.5 (2.5)
Empodisma minus RS	44							
Gymnoshoenus sphaerocephalus RS	29							
Leptospermum livesidgei RS	29	1	9					
Banksia oblongifolia RS	10	11	8	13				
Dillwynia floribunda OS	14	13	18	15				
Epacris obtusifolia OS	17	10	15	15				
Xanthorrhoea fulva RS	11	15	34	18				
Lepyrodia interrupta RS	32	4	59	36		16		
Darwinia leptantha OS	1	22	2	2		4	2	1
Pseudanthus orientalis RS		5	1	19	1		14	15
Persoonia lanceolata OS	4	20	5	6	1	4	1	3
Kunzea capitata OS	1	19		5		14		1
Dillwynia retorta OS					49		25	3
Leptospermum polygalifolium RS		6			1	3		
Leptospermum trinervium RS					24	5	15	6
Acacia ulicifolia OS					3		2	3
Banksia aemula RS				1	20	52	26	23
Melaleuca nodosa RS		1		2	13	3	20	13
Hypolaena fastigiata RS					10	7	15	4
Epacris pulchella OS						12		8

cover such as the banksias, *Banksia aemula* in dry heath and *B. oblongifolia* in wet heath. Wet heath had more cover from resprouting monocotyledons such as *Xanthorrhoea fulva* than dry heath, and more cover from obligate-seeding shrubs such as *Dillwynia floribunda* and *Epacris obtusifolia* with sparsely branched, elongate ascending stems. Though similar in depth to the watertable, the wet heath plots T2W1 and T3W1 differed in plant cover. T2W1 had high cover of *Empodisma minus* and *Gymnoschoenus sphaerocephalus*.

After the fire of January 1991, and sowing seeds in March 1991 under various treatments across the eight plots, as described in Myerscough et al. (1996), seedlings of *Banksia aemula*, *B. oblongifolia*, *Acacia ulicifolia* and *Dillwynia floribunda* differed in their patterns of survival across the plots (Table 3).

In dry heath plots, seedlings of *Dillwynia floribunda*, though fairly numerous at six months, suffered heavy mortality and were completely absent after four years. They persisted in all wet heath plots with approximately 10% of the population observed at six months present six years later, with some plants observed to have flowered after three and half years. All the plants in the plots were killed by the fire of January 1998. In short, it was only in the wet heath plots that plants of *D. floribunda* survived and reproduced, doing so with little plot to plot variation apparent in their survival (Table 3). Seven and a half years after the fire in January 1998, *D. floribunda* was among emergent species in the canopy of the wet heath plots (Table 4).

Some seedlings of *Acacia ulicifolia* survived from 1991 in each of the eight plots until the fire of January

Table 4. Experimental plots and height (m) of canopy (mean (SE)), emergent species and relative shading (*RSh) of banksia seedlings (numbers in each category) in September 2005.

Plot		T2W1	T2W3	T3W1	T3W2	T2D2	T2D3	T3D1	T3D2
Canopy height		1.50 (0.06)	1.37 (0.06)	1.38 (0.06)	1.09 (0.07)	2.08 (0.14)	1.93 (0.16)	2.15 (0.16)	1.63 (0.08)
@ Emergent species - number of contacts out of 10 (but out of 9 for T2W3)		*D.fl* 3	*D.fl* 2	*D.fl* 1	*D.fl* 2	*B.ae* 3	*B.ae* 4	*B.ae* 4	*B.ae* 1
		L.li 3	*L.li* 1	*L.li* 7	*L.li* 1	*L.tr* 5	*L.tr* 1	*L.tr* 4	*L.tr* 4
		S.in 3	*S.in* 2		*S.sp* 1	*D.re* 2			
			P.la 1				*P.la* 3		*P.la* 3
		A.el 1					*L.po* 1		
			E.mi 1	*E.mi* 1	*E.ob* 2				*E.mi* 1
			B.ob 1	*B.ob* 1	*B.ob* 1		*A.te* 1		
					B.fa 1			*C.te* 1	
					M.n 1			*W.p* 1	
					X.fu 1				*K.ca* 1
B. aemula RSh	5	3		4					
	4	3		9	5		2		2
	3	3	4	5	31		9		5
	2		1	2	10	1	1		5
	1		1		1				
B. oblong-folia Rsh	5								
	4			2	2				
	3		1	1	1				
	2		2						
	1								

@ A.el – Acacia elongata; A.te – Acacia terminalis; B.ae – Banksia aemula; B. ob – Banksia oblongifolia; B.fa – Boronia falcifolia; C.te – Calytrix tetragona; D.fl – Dillwynia floribunda; D.re – Dillwynia retorta; E.mi – Epacris microphylla; E.ob – Epacris obltusifolia: K.ca - Kunzea capitata; L.li – Leptospermum liversidgei; L.po – Leptospermum polygalifolia; L.tr – Leptospermum trinervium: M.n – Melaleuca nodosa; P.la – Persoonia lanceolata; S.in – Sprengelia incarnata; S.sp – Sprengelia sprengelioides; W.p – Woollsia pungens; X.fu – Xanthorrhoea fulva.

* RSh: 5, >95%; 4, 95-75%; 3, <75-25%; 2, <25% shaded; 1, seedling's canopy unshaded.

Table 3. Number of seedlings surviving on experimental plots through time (years) since sowing in March 1991.

Time	0.47	1.52	2.01	3.41	4.59	5.56	6.56	7.64	8.53	9.68	10.56	11.58	12.69	13.58	14.57	15.64	16.67	17.65
A. ulicifolia																		
T2W1	54	42	33	22	7	5	3											
T2W3	52	39	22	17	10	10	10											
T3W1	70	38	30	14	4	3	3											
T3W2	66	44	22	4	1	1	1											
T2D2	43	14	10	4	2	2	2											
T2D3	43	17	17	13	11	10	10											
T3D1	52	29	25	19	14	14	14	13	13	12	12	11	8	8	8	8	5	5
T3D2	55	15	14	12	5	5	3	3	3	3	3	3	1	1	1	1		
D. floribunda																		
T2W1	407	290	251	107	87	58	48											
T2W3	505	256	175	82	50	39	35											
T3W1	407	230	202	130	90	63	36											
T3W2	960	392	320	127	118	121	90											
T2D2	120	2	1															
T2D3	92	3																
T3D1	85	3	1															
T3D2	223	7	1	1														
B. aemula																		
T2W1	24	25	27	22	22	21	21	13	13	13	12	12	12	10	9	7	5	4
T2W3	47	45	47	10	9	9	9	6	6	6	6	6	6	6	6	6	6	6
T3W1	32	35	30	31	30	30	30	23	23	23	22	21	21	20	20	18	14	12
T3W2	73	65	68	62	61	61	61	51	50	48	48	48	47	47	47	45	44	44
T2D2	52	22	22	17	17	17	15	2	2	2	2	2	1	1	1	1	1	1
T2D3	54	51	54	48	47	46	44	12	12	12	12	12	12	12	12	12	10	10
T3D1	45	16	10	4	3	3	2	1	1	1								
T3D2	59	41	44	17	17	17	17	14	14	14	13	13	12	12	12	12	10	10
B.oblongifolia																		
T2W1	283	277	265	205	171	133	95	15	12	9	9	3						
T2W3	287	276	266	84	60	49	43	10	10	10	10	7	7	7	7	7	7	7
T3W1	284	241	240	182	149	110	86	18	18	18	18	12	12	9	9	9	9	9
T3W2	447	420	439	202	169	135	101	11	11	11	11	11	11	11	11	11	8	8
T2D2	94	16	13															
T2D3	126	73	67	48	40	37	28											
T3D1	65	14	5	4	1													
T3D2	160	50	35	2	1	1	1											

1998 burned six of the plots. Though survival varies considerably with plot, there is no clear pattern in this variation in relation to habitat or other characteristics of plots. In the two plots not burned in 1998, one plant continued to survive in T3D2 until it was fifteen and a half years-old, while in T3D1 five plants were still alive at 17.65 years (Table 3), four of them having fruited in 2008. In this plot, four-year-old plants flowered and fruited, and four-year-old plants were seen flowering on other plots (T2D3 and T2W3).

In *Banksia oblongifolia*, some seedlings survived on each of the eight plots up to two years (Table 3). On dry heath plots, they had died out after 5 years on both plots where the watertable was deep (T2D2 and T3D1) but continued to survive in significant number on T2D3, the dry heath plot with the least depth to the watertable (Table 2). No seedling of *B. oblongifolia* survived the fire of January 1998 on a dry heath plot, but on each of the four wet heath plots some seedlings survived. On T2W1, the plot with high cover of *Gymnoschoenus sphaerocephala* and *Empodisma minus* (Table 2), no seedling survived twelve years, but on the other three wet heath plots some seedlings survived up to seventeen years (Table 3).

In *Banksia aemula*, some seedlings survived on each of the eight plots up to nine and half years, including on the six plots totally burnt in the fire of January 1998. Their numbers were lowest on the two dry heath plots (T2D2 and T3D1) where the watertable was deep and cover of *Leptospermum trinervium* relatively high (Table 2). On T3D1, which had the deepest watertable (Table 2) and which was not burnt in 1998 (Table 1), the last survivor had died after ten years. On each of the other seven plots, at least one plant survived to seventeen years (Table 3). Among wet heath plots, there was heavier mortality of survivors of the fire of January 1998 on T2W1 and T3W1 (see years 7.64 to 17.65 in Table 3), plots with the shallowest watertable and highest cover of resprouting monocots (Table 2), than on T2W3 and T3W2. On T2W3 and T3W2, not only was the watertable deeper and the cover of monocots less (Table 2), but in September 2005 the surviving seedlings of *Banksia aemula* were less shaded (Table 4). There was one seedling of *B. aemula* on each of these plots that was unshaded (Table 4). On T2W3, one plant flowered at fourteen years and formed swollen follicles, and, after the fire in November 2006, six follicles appeared to have opened. This was the only banksia originating from seed in 1991 that was observed on any of the eight plots to have become reproductive.

Across the wet heath plots, mortality from the fire of 1 January 1998 was much higher among seedlings of *Banksia oblongifolia* (83%) than among those of *B. aemula* (23%) ($p<0.001$).

In both species of banksia, survival of seedlings on plots burnt in the fire of 1 January 1998 entirely depended on possessing a lignotuber; without a lignotuber no seedling survived (Table 5). Under comparable conditions in wet heath, the lignotubers of *B. aemula* survived better than those of *B. oblongifolia*. With the top of the lignotuber exposed, only 10% of seedlings of *B. oblongifolia* survived whereas 78% of those of *B. aemula* survived; with the lignotuber buried, 36% survived in *B. oblongifolia* and 95% in *B. aemula*. No tagged seedling of *B. oblongifolia* survived fire in a dry heath plot (Tables 3 and 5), while seedlings of *B. aemula* survived fire in both wet heath (WH) and dry heath (DH). The survival of *B. aemula* seedlings was much lower in DH (24%) than in WH (76%) not only because there was a higher proportion of seedlings without lignotubers in DH (24%) than in WH (7%) ($p<0.001$) but there was higher mortality of seedlings with lignotubers in DH (68%) than in WH (18%) ($p<0.001$). Burial of the lignotuber

Table 5. Number of tagged banksia seedlings live or dead in March 1998 after fire of 1 January 1998 in relation to habitat and lignotubers.

Species	*Banksia aemula*				*Banksia oblongifolia*			
Habitat	Dry heath		Wet heath		Dry heath		Wet heath	
Seedlings	Live	Dead	Live	Dead	Live	Dead	Live	Dead
Lignotuber:								
absent	0	14	0	8	0	5	0	5
present	14	30	93	21	0	10	19	117
Lignotuber top:								
buried	11	21	20	1	0	2	8	14
exposed	3	9	73	20	0	8	11	103

Table 6. Dimensions and relative shading (RSh) of grown tagged banksia seedlings in October 2007.

Species	*Banksia aemula*			*Banksia oblongifolia*		
Dimension	Mean lignotuber width (mm)	Plant height (cm)	Relative shading (RSh)@	Mean lignotuber width (mm)	Plant height (cm)	Relative shading (RSh)@
Dry heath plot T3D2	41	43	3			
Wet heath plots	41	14	2	23	16	2
T2W3	43	31	2	39	28	2
	74*	79*	1			
	53	76	1			
T3W2	37	72	1			

* Plant first flowered in 2005.
@ RSh: 1, seedling's canopy unshaded; 2, <25%; 3, <75-25% shaded

increased the chances of survival of seedlings, particularly in *B. oblongifolia*. In *B. aemula*, the extent of this was mediated by habitat. A higher proportion of lignotubers were buried in DH (73%) than in WH (18%) (p<0.001). Despite this, mortality of seedlings with buried lignotubers was much higher in DH (66%) than in WH (5%) (p<0.001), whereas seedlings with lignotubers exposed above ground suffered 75% mortality in DH and 22% mortality in WH (p<0.001). In short, though burial of their lignotubers enhanced survival of seedlings in both habitats, it was more effective in WH than DH though the proportion of seedlings with buried lignotubers was lower in WH than DH.

Of those tagged banksia seedlings surviving to October 2007, appreciable growth was detected in relatively few (Tables 6 and 7), and most of these seedlings occurred in one wet heath plot, T2W3. Indeed, in this plot, two of the three surviving seedlings of *Banksia oblongifolia,* and four of the six surviving seedlings of *Banksia aemula* had grown, with one of them flowering in 2005 and producing an infructescence with a single swollen follicle. This individual was the only seedling to have had a lignotuber over 40 mm in width by March 1998; no others had achieved this by September 2005. In March 2007, it had four infructescences on which a total of six follicles had opened after the fire in November 2006. This was the only tagged banksia seedling to have reached reproductive maturity. In all the other plots, there were only two tagged banksia seedlings that could be identified as having grown, both *B. aemula*, one on a dry heath plot, T3D2, and the other on a wet heath plot, T3W2. The rest of the surviving tagged banksia seedlings appeared to be simply surviving without net growth, and on the wet heath plot T3W2 such seedlings of *B. aemula* were particularly numerous (Table 7). In October 2007, all seedlings deemed to have grown were unshaded or <25% shaded (Table 6), except for the seedling on T3D2, a plot largely unburnt by the fire of November 2006 (Table 1).

All the tagged banksia seedlings surviving in October 2007 had originated on quadrats sown in March 1991 with seed of their own species, except for three seedlings; a seedling of *Banksia aemula* on T2D3, another on T3W2 and a seedling of *B. oblongifolia* on T3W1 (Table 8). All six seedlings of *B. aemula* that had grown since their lignotubers were first recorded (Table 6) had each originated from seed sown and then shallowly buried (Table 8). In wet heath plot T3W2, the pattern of survival of the relatively numerous seedlings of *B. aemula* in October 2007 appears to reflect reasonably closely the original 4:6:4 ratio in March 1991 of seed buried: seed sown on disturbed surface: seed sown on undisturbed soil surface among the quadrats on the plot (Table 8).

Table 7. Dimensions (mean (S.E.)) of tagged banksia seedlings deemed not to have grown between first recorded presence of lignotuber (in November 1995 unless otherwise indicated) and October 2007.

Species	*Banksia aemula*				*Banksia oblongifolia*			
	Number of plants	Initial lignotuber width (mm)	2007 lignotuber width (mm)	Plant height in 2007 (cm)	Number of plants	Initial lignotuber width (mm)	2007 lignotuber width (mm)	Plant height in 2007 (cm)
Dry heath plots								
T2D2	1	20	33	20				
T2D3	10	15 (2)	19 (2)	20 (2)				
T3D2	9	15 (1)	22 (3)	16 (3)				
Wet heath plots								
T2W1	5	18 (2)	16 (1)	7 (1)				
T2W3	2*	17	15	11	1	17	16	15
T3W1	14	23 (2)	22 (2)	12 (2)	3	14 (1)	12 (3)	13 (3)
T3W2	43@	20 (1)	19 (1)	12 (1)	2*	12	11	8

* 1 plant first record of lignotuber in March1998; @ 4 plants first record of lignotuber in November 1996, and 4 in March 1998.

DISCUSSION

Fire and habitat interaction

Fire and habitat variation interact in different ways across the four species of this study. The interaction is more complex in the two resprouting species than in the two obligate-seeding species.

Of the two obligate-seeding species, *Dillwynia floribunda* has the more straightforward relation with habitat and fire. After fire, seedlings emerge from seeds whose dormancy has been broken by heat, as in *Acacia ulicifolia* (Auld and O'Connell 1991). Though its seedlings can appear in dry heath, they only survived to maturity in wet heath (Table 3). In wet heath, its soil seed-bank was found by Myerscough et al. (1996) to be abundant, survival of plants after six months was high (Table 3), it was seen to be in flower three and a half years after fire and to be one of the emergent species in the canopy seven and a half years after fire (Table 4). It is one of a suite of obligate-seeding species with soil seed banks and similar sparsely branched erect stems with microphyllous leaves that emerge above resprouting monocotyledons characteristic of wet heath. Other such species are the heaths *Epacris microphylla*, *E. obtusifolia*, *Sprengelia incarnata*, *S. sprengelioides*, some of which occur with *D. floribunda* in fire-prone wet heaths on sandstones in the Sydney region (e.g., Keith and Myerscough 1993, Keith 1994, Keith et al. 2007a).

Seedlings of *Acacia ulicifolia* arose in both wet and dry heath particularly after shallow burial of heat-treated seed (Clarke et al. 1996). Survival varied among plots in both wet and dry heath, but there

Table 8. Number of tagged banksia seedlings live in October 2007 (grown: plants deemed to have grown; dwarfs: plants deemed not to have grown since their lignotubers were first recorded) in relation to how their seed was placed in March 1991 on or within the soil.

Species		*Banksia aemula*			*Banksia oblongifolia*	
Seed placed	Buried	Surface disturbed	Surface not disturbed	Buried	Surface disturbed	Surface not disturbed
Dry heath plots						
T2D2 dwarf	1					
T2D3 dwarfs	2	5*	3			
T3D2 dwarfs	1	4	4			
grown	1					
Wet heath plots						
T2W1 dwarfs	1	4				
T2W3 dwarfs	1	1			1	
grown	4			1	1	
T3W1 dwarfs	7	6	1		2*	1
T3W2 dwarfs	12	19	12*			2
grown	1					

* includes one seedling that arose in a quadrat not sown with seed of that species.

was at least one survivor in each plot immediately before the fire in January 1998 burned six of the plots (Table 3). Some plants were observed to flower at about three and a half years old, and, in an unburnt dry heath plot, plants flowered and set fruit until they were at least seventeen years old. The seedlings are, compared to those of *Dillwynia floribunda*, slow to gain in height, and are quickly overtopped in wet heath by resprouting monocotyledons, such as *Gymnoschoenus sphaerocephalus* in T2W1. A modest seed bank of *A.ulicifolia* was shown to occur in dry heath but none was found in wet heath (Myerscough et al. 1996). Thus, in wet heath, lack of seed and, for any seed reaching it, scarcity of conditions for successful seedling emergence appear to exclude *Acacia ulicifolia*, and occurrence of the species is confined to dry heath where it has a soil seed bank, suitable conditions occur after fire for germination of seed and emergence of seedlings, and seedlings are less readily overtopped by other understorey species.

Thus *Dillwynia floribunda* and *Acacia ulicifolia* are excluded from each other's characteristic habitat early in the life cycle, though at different stages; *A. ulicifolia* through lack of available seed and suitable safe sites (sensu Harper 1977) for any rare seeds present in wet heath, and *D. floribunda* apparently by lack of suitable growing conditions for seedlings in dry heath. In short, their respective distributions relate to their regeneration niches (sensu Grubb 1977). Beyond the regeneration stage, they need to reproduce successfully in their respective habitats, which observations in this study, while not detailed, indicate occurs, with some seedlings of each species in their fourth year probably contributing seed to the soil seed-bank.

This study reveals that in this coastal heath the two resprouting species have three critical phases in their life cycle, regeneration, persistence and growth. What happens to individual plants as they enter and pass through each phase and make transition from one stage to the next depends on fire and habitat. This differs between the two species. Transition from seedling to persistent plant is made evident through fire, while that from fire-resistant but merely persistent plants to plants growing toward reproductive capability is more gradual, presumably depending on success in garnering necessary resources.

In the regeneration phase, patterns of seedling establishment between habitats (Myerscough et al. 1996) and among experimental treatments and plots within habitats (Clarke et al. 1996) differed between *Banksia aemula* and *B. oblongifolia*. Seedlings of *B. oblongifolia* that arose in dry heath were fewer and died earlier than on wet heath plots, and, though several survived on T2D3 for six and a half years, none survived the fire in January 1998 (Table 3). In contrast, survival of *Banksia aemula* occurred across both habitats, and on all the wet heath plots and on three of the dry heath plots there was at least one survivor after seventeen years (Table 3). Survival of seedlings of *B. aemula* was least on dry heath plots (T2D2 and T3D1) with low water tables (Tables 2 and 3).

The fire of 1 January 1998 caused mortality among seedlings of both species, but mortality was much greater in *B. oblongifolia* than in *B. aemula*. Overall, in the wet heath plots, 77% of seedlings of *B. aemula* survived the fire while only 17% did in *B. oblongifolia*. In both species, to persist through the fire a lignotuber was essential (Table 5). Lignotubers had formed by four and a half years from the sowing of the seed on most of the seedlings that survived, but some had formed somewhat later (Table 7). One factor in the lower survival of seedlings of *Banksia oblongifolia* is the structure of the lignotubers its seedlings form. They are small and lack the thick corky bark of the larger lignotubers of the seedlings of *B. aemula*. In *B. oblongifolia* many of the unburied lignotubers formed completely above the ground surface while this did not occur in seedlings of *B. aemula*; in them, a lower part was at least in the ground. In both species, as Auld (1987) showed in seedlings of *Angophora hispida*, burial of the lignotuber enhanced survival of the seedlings, though again to a greater extent in *Banksia aemula* than in *B. oblongifolia*. In short, the lignotubers of seedlings of *B. aemula* appear to be better insulated than those of seedlings of *B. oblongifolia*, and the transition of seedlings through fire to the fire-resistant persistent phase is made with much less mortality in *B. aemula* than in *B. oblongifolia*.

In each of the banksia species, very few of the surviving seedlings showed detectable growth between March 1998 and September 2007. Most of them appeared to be simply persisting without detectable net growth. They seem to be in a prolonged "sit-and-wait" state, ageing juvenile plants that Silvertown (1982) called oskars. In many plant communities, growth of such oskars is restricted by lack of sufficient light. Though some shading occurs in the heaths, especially wet heath with abundant monocots in the understorey (Tables 2 and 4), lack of growth in these banksia seedlings is not solely related to light (Table 4). Indeed light was abundant at ground level for several weeks after fire, as occurred when the seedlings arose from seed in 1991 and immediately following their survival through the fire of 1 January 1998. If their growth is resource-limited, the critical resources are those in the soil. Water is probably readily available across the range of habitats, though water stress may be a factor in dry heath with deeper water tables (Table 2). The limiting resources are likely to be one or more of the mineral nutrients needed for plant growth. Previous work (Myerscough and Carolin 1986) has indicated that the sands on which these heaths occur are very low in mineral nutrients. Circumstantial evidence that shortage of mineral nutrients retarded growth of the seedlings comes from the seedlings that grew. All except two were from the wet heath plot T2W3. On this site, when holes were drilled to observe the watertable, a very consolidated coffee rock, B horizon, was reached at c. 0.5 m in three of the four holes. In other wet heath plots, B horizons were deeper and less consolidated. Data of Griffith et al. (2004) indicate that roots of seedlings of both species of banksia, particularly *B. aemula*, may grow down to B horizons fairly rapidly in similar heaths. It is thus possible that banksia seedlings on this plot could reach the B horizon relatively easily and extract nutrients from it. Furthermore, the plant that grew early and reached reproductive maturity was relatively near one of the holes that had pierced the B horizon to observe the watertable; the disturbance of the hole may have released nutrients that accelerated its growth. Incidentally, this individual flowered when it was less than a metre high (Table 6), showing no sign of requiring an elongated stem for flowering, as in *Banksia serrata* (Bradstock and Myerscough 1988). Its inflorescences were produced more or less sessile on a thickened main stem that was merely an upward extension of the thickening of the lignotuber. Other low-growing reproductive individuals of *B. aemula* on this sand system had a similar growth form, while taller growing individuals with trunks occur in sites such as T2D2 and T3D1, and, after fire, produce inflorescences on newly grown stems up to 1 m long.

Growth leading to mature reproductive individuals, persistence of fire-resistant juveniles and regeneration in terms of establishment of seedlings appear as fairly distinct phases in the life cycles of *B. aemula* and *B. oblongifolia*. Each phase has its characteristic relations with habitat and fire that differ between the species. In *B. oblongifolia*, its restriction to wet heath is clearly evident at the regeneration phase (Myerscough et al. 1996), and, as seen in this study, should seedlings survive in a dry heath site they tend to be eliminated in the first fire and thus never enter the phase of fire-resistant juveniles (Tables 3 and 5). Fire-resistant juveniles of *B. oblongifolia* occurred in wet heath plots, but in the plot, T2W1, having survived the fire of 1 January 1998, they were eliminated (Table 3), probably shaded out under the high cover of *Empodisma minus* and *Gymnoschoenus sphaerocephalus* (Table 2). In the other three wet heath plots some continued to survive to seventeen years, but only clearly entering the growth phase in one, T2W3.

In *Banksia aemula*, given availability of seed and modification of the soil surface (Myerscough et al. 1996, Clarke et al. 1996), seedlings arose and survived in all wet and dry heath plots. Ongoing survival was least in the two dry heath plots T2D2 and T3D1 (Table 3) with deep watertables. Transition through the fire of 1 January 1998 on six of the eight plots to persistent fire-resistant juveniles was made with high rates of survival, particularly in the wet heath plots (Table 3). The question arises as to whether the patterns seen at the regeneration stage in seedlings in relation to particular soil treatments applied at sowing of the seeds in March 1991 (see Clarke et al. 1996) were maintained or altered in subsequent survival. In T3W2, the plot with highest number of fire-resistant juveniles persisting at seventeen years, the indication is that the pattern seen in the regeneration phase in relation to soil surface disturbance and seed burial is retained at seventeen years in the persistence phase (Table 8). This plot incidentally was unique among the four wet heath plots in showing little effect of soil treatment and seed burial in numbers of seedlings surviving at the regeneration phase (see Fig. 2 of Clarke et al. 1996); the three other plots all showed that the greatest number of seedings arose from buried seeds. All six of the plants that were deemed to have entered the growth phase had arisen from buried seed (Table 8).

These findings give some insight into the status of populations of the two banksia species on the Eurundereee Pleistocene beach ridges. Firstly, they suggest that their population turn-over is very slow. Indeed, after seventeen years, there is little firm evidence of effective recruitment in either species. In *Banksia aemula*, only one surviving juvenile showed any evidence of growth in dry heath. While, in wet heath plots, there were numbers of persistent fire-resistant juveniles, a few of which grew, it was an artificial situation brought about by firstly unnaturally increased availability of seed, relative to naturally occurring levels of seed (Myerscough et al. 1996), and secondly by burial of seeds which is unlikely to occur readily in nature in wet heath (Clarke et al. 1996). In *Banksia oblongifolia*, very few seedlings survived the fire on 1 January 1998 and persisted as fire-resistant juveniles. The only two that grew arose from seed that in one case had been buried and in the other from seed on a disturbed surface (Table 8). Casual observation of existing mature individuals of either *B. aemula* or *B. oblongifolia* suggests that over the seventeen years there was little if any mortality among them. The picture then is of populations of mature long-lived individuals into which there is little opportunity for recruitment of juveniles. Secondly, it appears that, though juveniles may persist several years in a non-growing state, they are limited by lack of resources for growth to progress to mature plants. It is probable that on most plots, the limiting resources are soil nutrients. In the case of one wet heath site with cover of *Empodisma minus* and *Gymnoschoenus sphaerocephalus,* lack of light may eliminate juveniles of *Banksia oblongifolia*, even though mature plants of the species had appreciable cover (Table 2). This suggests that either the current mature plants recruited as seedlings before *E. minus* and *G. sphaerocephalus* were so abundant in the site, or, if they were present and abundant, fire frequency was so high that shade from them did not eliminate juveniles of *B. oblongifolia*.

Though the evidence indicates that, presently on these Pleistocene sand ridges, niches for effective regeneration, persistence and growth for these two resprouting species are rare, there must be periods when they are in colonising mode and these niches are more common. This would have been so for *B. aemula* when parts of Holocene dunes south of Mungo Brush between the Myall River and the sea were colonised by it. Their winged seeds, dispersed some distance in wind, as in those of *Banksia serrata* observed by Hammill et al. (1998), particularly in willy-willies as were seen to occur in the area of this study on the Pleistocene beach ridges after an intense fire in January 1991, appear well suited for the initial step in colonisation of new habitat.

Selection and mode of regeneration

The contrast is stark between the two obligate-seeding species studied in which in suitable habitat regeneration is followed very quickly by reproductive maturity of individuals, and the two resprouting species where formation of a fire-resistant lignotuber occurs early and fire-resistant individuals enter a period of persistence in which the majority in this study showed no demonstrable growth toward maturity. As Keith et al. (2007b) have pointed out, the resprouters thus show all the characteristics of Grime's (1979) stress-tolerators or Stearns' (1976) K-selected species, while the obligate-seeders are examples of Stearns' r-selected species. Whether, under selection, their breeding systems follow the suggestion of Heslop-Harrison (1964, Table IV, p. 200) that species with short life cycles, exemplified here by obligate-seeders, are more likely to be inbreeders while species with longer life cycles and slowly maturing adults, exemplified by resprouters, are more likely to be out-breeders would be interesting to establish.

It is possible that paths to extinction may differ between obligate-seeders and resprouters. Resprouters may lose effective reproduction through seedlings and reach a terminable state of a few mature long-persisting individuals, perhaps propagating as clones, while high levels of inbreeding may lead to extinction in some obligate-seeders. How far, in fire-prone habitats, general differences exist between obligate-seeders and resprouters in degrees of in and out-breeding, and thus levels of heterozygosity of individuals, is a question that is yet to be investigated.

There is an indication in Table 2 that the species with high cover ten years from fire in both habitats are either strongly obligate-seeding or resprouting, with the possible exception of *Pseudanthus orientalis*. This would support the suggestion that, in vegetation subject to fairly frequent fires, as appears to have been so in these heaths (Myerscough and Clarke 2007), selection is strong for individuals and thus species to be either markedly obligate-seeding or strongly resprouting and against individuals and species that are neither markedly one nor the other. To establish this as a general rule would require further work.

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